PAPPUS VARIATION IN *SOLIDAGO* (ASTERACEAE: ASTEREAE)

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ABSTRACT

The pappus in the goldenrod genus *Solidago* (Asteraceae: Astereae) was examined in 75 species and compared with variation in 14 species of 12 related genera in subtribe Solidagininae in the narrow sense following Nesom (2000) and three species of asters of two genera basal to the North American Clade of the tribe. *Solidago* has been described as having a simple pappus consisting of one whorl of barbellate bristles with the exception of a few species in several sections, sometimes treated as distinct genera. Species of *Solidago* sect. *Corymbosae* (*Oligoneuron*) have long been recognized as having a biseriate pappus with clavate bristles similar to that of other genera of the subtribe. However, nearly all species of *Solidago* displayed some evidence indicating the pappus bristles occur in two more or less heteromorphic whorls of bristles, here designated as the primary outer whorl and the primary inner whorl. A few species also occasionally had a third, much shorter secondary outer whorl of a few bristles. In the most heteromorphic species, the primary outer whorl of bristles was slightly shorter and had tips that gradually tapered. The primary inner whorl of slightly longer bristles had distinctly clavate tips up to several times as broad as the bristle below the tip. As well, the bases of the primary outer whorl were clearly external to those of the primary inner clavate whorl in some species. In contrast, most species in several subsections of the genus exhibited little evidence of a biseriate pappus or clavate bristle tips. The pappus of each species was scored on several traits: 1) non-clavate to distinctly clavate bristle tips, 2) evidence of alternating non-clavate and clavate bristles or shorter and longer bristles, and 3) evidence of overlapping primary outer and inner whorls of bristles. One species of *Solidago* had an atypically short pappus; the bristles of *S. sphacelata* were less than half the length of the cypsela body. The biseriate pappus of *Brintonia discoidea* was usually tinted with anthocyanotic pigments unlike any species of *Solidago*; the species has been included in *Solidago* by some authors.

RESUMEN

Se examinó el vilano en 75 especies del género *Solidago* (Asteraceae: Astereae) y se comparó con la variación en 14 especies de 12 géneros relacionados de la subtribu Solidagininae en sentido restringido según Nesom (2000) y tres especies de asteráceas de dos géneros basales al clado Norte Americano de la tribu. *Solidago* se ha descrito como poseedor de un vilano simple que consiste en un verticilo de sedas barbeladas, con la excepción de unas pocas especies en varias secciones, a veces tratadas como géneros diferentes. Las especies de *Solidago* sect. *Corymbosae* (*Oligoneuron*) han sido reconocidas por presentar un vilano biseriado con sedas clavadas similares a las de otros géneros de la subtribu. Sin embargo, casi todas las especies de *Solidago* muestran algunas pruebas que indican que las sedas del vilano se sitúan en dos verticilos más o menos heteromórficos, que aquí se nombran como verticilo primario externo y verticilo primario interno. Unas pocas especies también tienen ocasionalmente un tercer verticilo, el verticilo secundario externo, mucho más corto y de unas pocas sedas. En la

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especie más heteromórfica, el verticilo primario externo de sedas era ligeramente más corto y tenía extremos gradualmente afilados. El verticilo primario interno, de sedas ligeramente más largas, tiene extremos claramente clavados de hasta varias veces más anchos que la propia seda debajo del extremo. Así mismo, las bases del verticilo primario externo eran claramente externas a las del verticilo primario interno clavado en algunas especies. Por contra, la mayoría de las especies de varias subsecciones del género mostraban pocas pruebas de un vilano biseriado o de extremos de las sedas clavados. El vilano de las distintas especies fue escrutado en varios aspectos: 1) extremos de las sedas de no-clavadas a distintamente clavadas, 2) evidencia de alternancia de sedas no-clavadas y clavadas o sedas más cortas y más largas, y 3) evidencia de solapamiento de los verticilos de sedas primario externo e interno. Una especie de *Solidago* tenía un vilano atípicamente corto; las sedas de *S. sphacelata* eran menos de la mitad de la longitud del cuerpo de la cipsela. El vilano biseriado de de *Brintonia discoidea* estaba normalmente teñido con pigmentos antociánicos, cosa que no ocurre en las especies de *Solidago*; la especie ha sido incluida en *Solidago* por algunos autores.

INTRODUCTION

Previously the genus *Solidago* L. was considered different from closely related genera in regards to its pappus characteristics. While related taxa such as *Sericocarpus* Nees, *Tonestus* A. Nels., *Petradoria* E.L. Greene, *Chrysothamnus* Nutt. and *Ericameria* Nutt. were considered to have a pappus in 2–3 series (1–2 for *Tonestus*), the genus *Solidago* was stated to have a pappus in a single series (e.g., Semple et al. 1999; Nesom 2000). It has also been described as simple (Fernald 1950; Correll et al. 1970). Some treatments do not mention anything about the seriate nature of the pappus in the genus description (Radford et al. 1968; Cronquist, 1980; Gleason and Cronquist 1991), although variations are indicated in species descriptions. Some treatments state that the pappus of *Solidago* exhibits some variation. Gleason and Cronquist (1991) recorded the pappus as being "of numerous equal or sometimes unequal capillary bristles" for species from the northeast U.S.A. and adjacent Canada, while Cronquist (1994) noted the pappus as being "equal or sometimes somewhat unequal" in Great Basin species. Some of the differences in description are due to differences in which taxa were included in the genus *Solidago*, particularly the generally recognized clavate tipped members of *Solidago* sect. *Corymbosae* Torrey & A. Gray. For example, Cronquist (1980) included these flat-topped goldenrods, but excluded *Brintonia discoidea* (Elliott) E.L. Greene, the Mock Goldenrod. In contrast, Nesom (2000) excluded the former species placing them in the genus *Oligoneuron* Small, but included *Brintonia discoidea* as *S. discoidea* (Elliott) Torrey & A. Gray. Nesom (1991) discussed morphological reasons for treating *B. discoidea* within *Solidago*. Semple (submittted) treated *Brintonia* as a separate genus based on morphology (phyllary traits, disc corolla traits, pappus traits), field observations and DNA studies (Beck and colleagues, pers. comm.). *Solidago sphacelata* Raf. has been treated as *Brachychaeta sphacelata* (Raf.) Britt. due to its distinctive short pappus, but the general consensus recently is to retain it within *Solidago* (Cronquist 1980; Nesom 1991, 1993; Semple and Cook, submitted). Other authors in the past have included *Euthamia* (Nutt.) Nutt.,

Oreochrysum Rydberg, or *Petradoria* in *Solidago*, there by increasing the range of variation in pappus traits within the latter genus (e.g., Fernald 1950; Kearney & Peebles 1951; Harrington 1964; Semple et al. 1999).

The details of pappus bristle shape have generally been overlooked and descriptions have included various terms. Most have described the pappus of *Solidago* as "capillary" or "hair-like" (Fernald 1950; Radford et al. 1968; Correll & Johnston 1970; Cronquist 1980, 1994; Gleason & Cronquist 1991). Some treatments mention the pappus of *Solidago* as being "barbellate" or "clavate" in some species (Cronquist 1980, *S. ptarmicoides* (Torrey & A. Gray) Boivin; Semple et al. 1999, *S. houghtonii* Torrey & A. Gray, *S. ptarmicoides* (as *S. asteroides* Semple), *S. sempervirens* L.). Pappus bristles of *Solidago* and closely genera have been described as being "barbellate" (Nesom 2000). Nesom (1993) in his overview of *Solidago* and *Oligoneuron* used pappus bristle apex features as taxonomic characters: "strongly clavate," "attenuate," and "slightly but distinctly dilated toward the apex." He listed these in descriptions of sections and subsections, and noted the character state of pappus bristles for some species in particular.

The occurrence of a biseriate to multiseriate pappus has long been reported in other genera in the Tribe Astereae in both the North American Clade, which includes *Solidago* (see Semple et al. 2002), and the Basal Grade of South American and Old World Genera. The more basal genera in the North American Clade are biseriate or triseriate with bristles of equal or different lengths. These include most of the genera included traditionally in the Old World genus *Aster* L.: *Doellingeria* Nees, *Eucephalus* Nutt., *Ionactis* E.L. Greene, *Oclemena* E.L. Greene, *Sericocarpus*. Most species in subtribe Chrysopsidinae Nesom are biseriate, having a short outer whorl and a much longer inner whorl. In contrast, the pappus of some genera is typically uniseriate, e.g. *Symphyotrichum* Nees. In some cases the usual barbellate bristles are absent or very reduced, e.g. ray floret cypselae of *Heterotheca* sect. *Heterotheca*, *Aphanostephus* DC. The number of bristles varies greatly between species within and between genera as well. Thus, within the North American Clade of genera of Astereae there exists a range in the number of whorls, their relative lengths and their shapes (see Nesom 2000 for general descriptions of genera). No detailed systematic examination of the pappus of most or all species of *Solidago* has been reported. Our study was undertaken to fill in this gap in knowledge.

MATERIALS AND METHODS

A preliminary survey was undertaken to examine under the dissecting microscope the pappus bristles of one or two specimens of representative species of the sections and subsections of *Solidago*. Subsequently, a more rigorous survey was conducted involving 75 species of *Solidago* and 17 species of 14 other genera listed in Table 1. Two methods of observation were employed, and a system of ranking the degree of the clavateness of bristle tips was developed. Most ob-

TABLE 1. Pappus characteristics of *Solidago* taxa and related genera.

Taxon	Clavate[1]	Alternating	Overlapping	Comments
SOLIDAGO* L. sect. *SOLIDAGO				
subsect. ***Solidago***				
S. virgaurea	3	Yes	Yes (random)	
subsect. ***Multiradiatae*** (Juzepczuk) Semple				
S. cutleri	3	Yes	Yes (slight)	
S. multiradiata	2	Yes	Yes (slight)	
S. spithamea	2	Yes	Yes	
subsect. ***Humiles*** (Rydberg) Semple				
S. arenicola	4	Yes	Yes (random)	
S. kralii	4	Yes	Yes (slight)	short obscure secondary outer whorl
S. plumosa	1	Yes	Yes (random)	
S. simplex	3	Yes	Yes (random)	
S. spathulata	1	Yes	Yes (random)	
subsect. ***Thyrsiflorae*** (A. Gray) Nesom				
S. buckleyi	4	Yes	Yes	thickened length
S. hintoniorum	2	Yes	Yes	much overlapping of bases
S. orientalis	3	Yes	Yes	much overlapping of bases
S. petiolaris	3	Yes	Yes (slight)	
S. wrightii	2	Yes	Yes (random)	
subsect. ***Albigula*** (Raf.) Nesom				
S. bicolor	4	Yes	Yes	Overlapping very distinct in places
S. erecta	4	Yes	Yes	possible secondary outer whorl, very thickened tips
S. hispida	3	Yes	Yes (slight)	
S. puberula	3	Yes	Yes	
S. roanensis	2	Yes	Yes (random)	
S. sciaphila	3	Yes	Yes	
S. speciosa	4	Yes	Yes	
S. squarrosa	3	Yes	Yes (random)	bristles highly crowded at base
subsect. ***Glomeruliflorae*** (Torrey & A. Gray) Nesom				
S. albopilosa	3	Yes	No	
S. caesia	2	Yes	Yes (slight)	
S. curtisii	3	Yes	No	
S. flexicaulis	3	Yes	Yes	
S. glomerata	3	Yes	Yes (slight)	
S. lancifolia	3	Yes	Yes (slight)	
S. macrophylla	2	Yes	No	very large cypselae
subsect. ***Argutae*** (Mackenzie) Nesom				
ser. ***Argutae*** (Mackenzie in Small) Nesom				
S. arguta	4	Yes	Yes (random)	seemingly short pappus
S. fauciba	2	Yes	Yes (slight)	
S. ludoviciana	2	Yes	Yes (slight)	
S. patula	2	Yes	Yes	

Taxon	Clavate[1]	Alternating	Overlapping	Comments
ser. ***Auriculatae*** Semple				
S. auriculata	3	Yes	Yes	
ser. ***Brachychaeta*** (Torrey & A. Gray) Nesom				
S. sphacelata	1	Yes	No	very reduced; alternating very short and short bristles
subsect. ***Junceae*** (Rydberg) Nesom				
S. confinis	1	Yes	Yes	thick bristles, long-short alternation, pronounced overlap
S. gattingeri	0	Yes	No	
S. guiradonis	2	Yes	Yes	
S. juncea	1	Yes	No	
S. missouriensis	0	Yes	No	long-short alternation, some longer bristles are thicker
S. pinetorum	1	Yes	No	
S. spectabilis	1–2	Yes	No	thickened tips, crowding at base
subsect. ***Maritimae*** (Torrey & A. Gray) A. Gray				
S. sempervirens	2	Yes	Yes	reduced secondary outer whorl (subsp. *sempervirens* and *mexicana*)
S. stricta	2	Yes	Yes	(subsp. *stricta* and *gracillima*)
S. pulchra	2	Yes	Yes (slight)	thickened length, very reduced secondary outer whorl
S. uliginosa	1	Yes	Yes (slight)	
subsect. ***Venosae*** (G. Don in Loudon) Nesom				
ser. ***Venosae***				
S. ulmifolia	0	Yes	Yes	overlapping very distinct at times; alternating short and long bristles
S. delicatula	1	Yes	Yes (random)	
S. latissimifolia	1	Yes	Yes (slight)	some prominent overlap at base of whorls
S. rugosa	1	Yes	No	
S. fistulosa	1	Yes	No	crowding at base
ser. ***Odorae*** (Mackenzie) Semple				
S. odora	2	Yes	Yes	long-short alternation, strong overlap, possible secondary outer whorl
subsect. ***Triplinervae*** (Torrey & A. Gray) A. Gray				
S. altiplanities	1–2	Yes	Yes (slight)	
S. altissima	0	No	No	possibly alternating, but only very weakly (both subspecies)
S. canadensis	0	No	No	possibly alternating, but only very weakly

TABLE **1.** cont.

Taxon	Clavate[1]	Alternating	Overlapping	Comments
S. elongata	2	Yes	Yes (random)	
S. gigantea	0	No	No	
S. juliae	1	Yes	Yes (random)	
S. leavenworthii	1	Yes	Yes (random)	
S. lepida				
subsp. *fallax*	1	Yes	No	
subsp. *lepida*	1	Yes	No	(var. *lepida* and var. *salebrosa*)
S. muelleri	1	Yes	No	
S. shortii	2	Yes	Yes (slight)	
S. tortifolia	0	Yes	No	
subsect. ***Nemorales*** (Mackenzie) Nesom				
S. nana	3	Yes	Yes	
S. nemoralis	1	Yes	No	(subsp. *nemoralis* and *decemflora*)
S. mollis	2	Yes	No	
S. radula	2–3	Yes	No	
S. velutina				
subsp. *californica*	2	Yes	No	
subsp. *sparsiflora*	1–2	Yes	Yes (slight)	
subsp. *velutina*	2	Yes	Yes (slight)	
***SOLIDAGO* L. sect. *CORYMBOSAE* Torrey & A. Gray**				
S. houghtonii	2	Yes	Yes	
S. nitida	3	Yes	Yes	
S. ohioensis	3	Yes	Yes	
S. ptarmicoides	4	Yes	Yes	
S. riddellii	2	Yes	Yes	
S. rigida	2	Yes	Yes	strong overlapping (subsp. *rigida*, *humilis*, and *glabrata*)
placement uncertain				
S. ericamerioides	2	Yes	Yes (slight)	
Some Other Genera of the Solidagininae sensu Nesom (2000)				
Brintonia discoidea[2]	3	Yes	Yes (slight)	bristles tinted with anthocyanins; biseriate pappus
Chrysoma pauciflosculosa	2	Yes	Yes	strong overlapping; secondary outer whorl of much shorter tapering bristles; primary outer whorl slightly shorter bristles tapering to weakly clavate; primary inner whorl of longer somewhat clavate bristles

Taxon	Clavate[1]	Alternating	Overlapping	Comments
Chrysothamnus viscidiflorus	1	Yes	Yes	obvious biseriate pappus
Ericameria laricifolia	3	Yes	Yes	obvious biseriate pappus
Ericameria discoideum	1	Yes	Yes	biseriate pappus
Euthamia graminifolia	0	Yes	No	variation in bristle length obscures weak pattern of short-long alternation of bristles
Gundlachia corymbosa	0–2	Yes	No	weakly biseriate with the two whorls alternating; primary outer slightly shorter, tapering; primary inner longer, weakly clavate
Gutierrezia sarothrae	0	No	No	crown of irregular some-what erose scales of varying lengths and widths
Hesperadoria scopulorum	1	Yes	Yes	multiiseriate pappus; primary whorls of many Longer bristles, one shorter outer secondary whorl of fewer bristles
Oreochrysum parryi	1	Yes	Yes (slight)	
Petradoria pumila	1	Yes	Yes	obvious biseriate pappus
Sericocarpus				
S. linifolia	4	Yes	Yes	obvious biseriate pappus; outer whorl slightly shorter than inner
S. oregonensis	4	Yes	No	possible slight overlapping at base of whorls
Tonestus pygmaeus	4	Yes	Yes	
Genera Basal to the North American Clade				
Doellingeria umbellata	3	Yes	Yes	triseriate; short outer third whorl
Eucephalus				
E. breweri	2	Yes	Yes	triseriate pappus
E. elegans	4	Yes	Yes	biseriate, possible weakly triseriate

[1] arbitrary ranking of 0 (not clavate) to 4 (strongly clavate)

[2] treated as *Solidago discoidea* by Nesom (1993)

servations were made using a dissecting scope or a compound light microscope. Some observations were made using dried and gold coated specimens on a Hitachi S-570 Scanning Electron Microscope (SEM). At least five different fruits from each species were observed under the dissecting microscope at a maximum of 70×; most observations were made at 30×. In some cases multiple dozens of specimens of a species were examined. For the most part, observations were made on specimens in the WAT Herbarium, but additional material on loan from BRIT, F, GH, JEPS, NY, TEX and UC (Holmgren et al. 1990) was also examined.

Observations on the compound microscope were made from slides prepared as follows. For each species, two ray floret and two disc floret cypselae with corollas were mounted in DepeX mounting medium under a cover slip. Observations at 100× on the compound microscope were made similarly to the observations under the dissecting scope at 30×–70×. Observations made on the two kinds of scopes were compared and any discrepancies were resolved by re-examining specimens.

Each taxon was scored in the following manner:

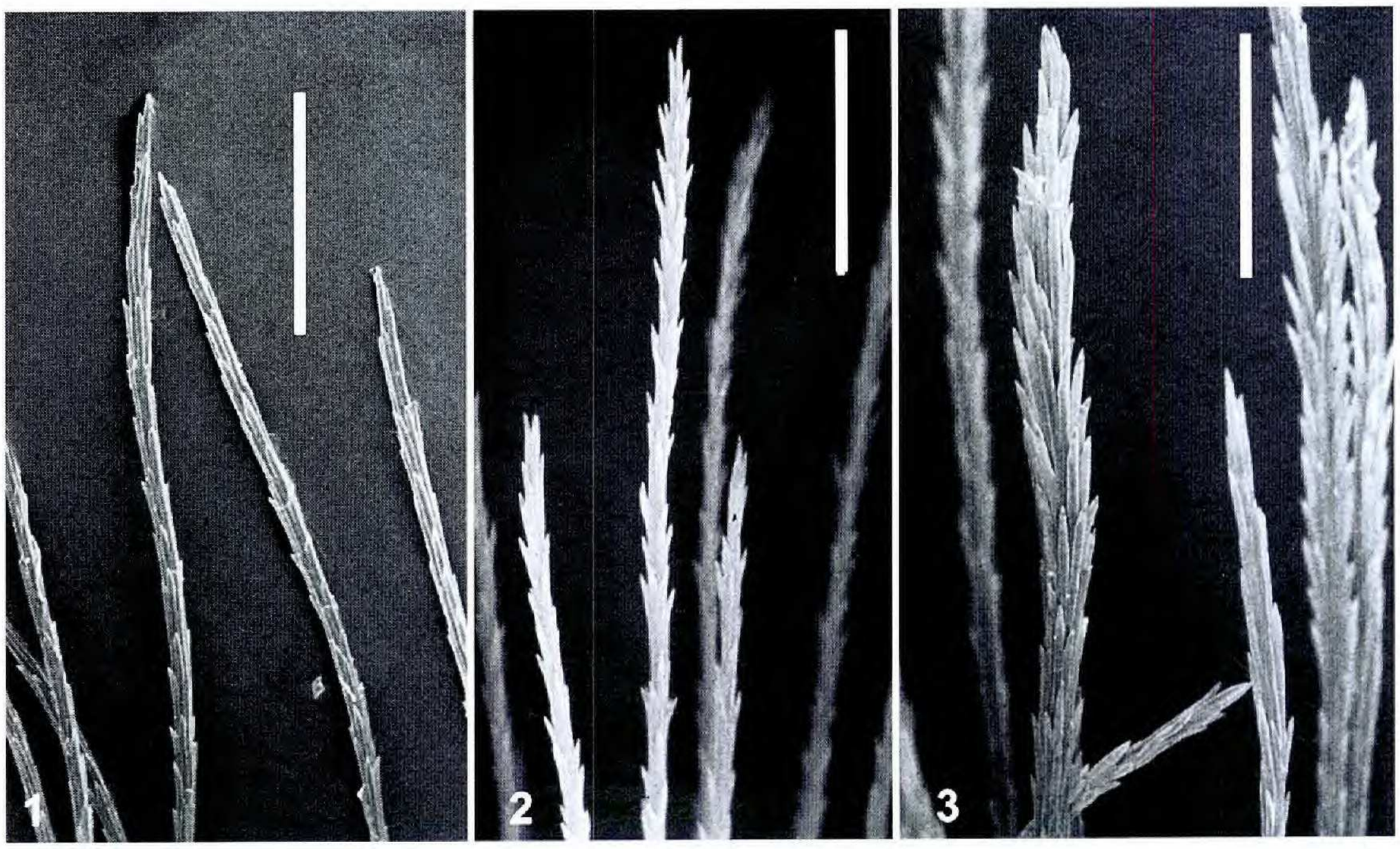
1. Cypselae were assigned a number from 0–4 depending on the thickness of the tip of the bristle in relation to the thickness along the length: 0 = no observable increase in thickness and the bristles tapered to a point (Fig. 1); 1 = a very slight increase in thickness near the tip, or the bristles not tapering gradually; 2 = a slight to moderate increase in thickness near the tip (Fig. 2); 3 = a strong and obvious presence of clavate tips; and 4 = very noticeable increase in thickness, very obvious clavate nature of the bristles (Fig. 3). A set of reference light-microscopy photomicrographs were used to maintain consistency in assigning values.

2. Cypselae were scored as showing no evidence of alternation of primary inner and outer whorls of bristles or as showing evidence of alternating with the notes on the nature of the alternation (No or Yes in Table 1, respectively).

3. Cypselae were scored for evidence of overlapping at the bases of the outer and inner whorls of bristles. The taxa examined were graded in three categories regarding the overlapping of the bristles at the base: Yes = complete overlap of bristles; Yes (slight) = slightly overlapping with outer whorl bristles consistently appearing external to inner whorl bristles; and Yes (random) = overlapping of some outer bristles external to inner bristles but not consistently so for the two whorls.

4. Notes were made when a secondary outer whorl (a third whorl) of very short barbellate bristles was observed. Such bristles were not easily observed and occurred in low numbers, thus the presence or absence of such bristles was not tabulated.

Digital photomicrographs were taken using a Nikon CoolPix 990 camera manually held against the ocular lens of either the dissecting or compound



FIGS. 1–3. Pappus bristle tip variation in *Solidago*; scanning electron micrographs, scale bar = 0.3 mm. **1.** Non-clavate bristle tip, *S. pinetorum* (0 value in Table 1). **2.** Weakly clavate bristle tip, *S. odora* (2 value in Table 1). **3.** Strongly clavate bristle tip, *S. erecta* (4 value in Table 1).

microscope. Pictures were taken of specimens under the compound light microscope with either below stage or above stage lighting. SEM photomicrographs were made using Ilform Pan F film commercially developed and subsequently digitized by scanning the negatives. Final digital illustrations were made using CorelDraw 10® from digital images edited with Corel PhotoPaint10® (Corel Corp.).

RESULTS AND DISCUSSION

The lack of a standard set of terms for pappus bristle whorls in *Solidago* and other genera lead to some confusion in discussing the results between the authors and for the reviewer. The following labels are presented as potential future "standard" terms for discussing pappus whorls in the Astereae. Because a biseriate pappus is found in many genera of the tribe, we recommend that these two whorls of bristles be referred to as the "primary outer whorl" and the "primary inner whorl." The primary inner whorl often is longer and has slightly to strongly clavate bristle tips. The third, often much shorter, outer whorl present in some genera can be referred to as the "secondary outer whorl." These labels for bristle whorls are used consistently throughout this paper. The term "secondary" with appropriate modifiers can be applied to any additions whorls, e.g. a secondary innermost whorl of non-clavate long bristles.

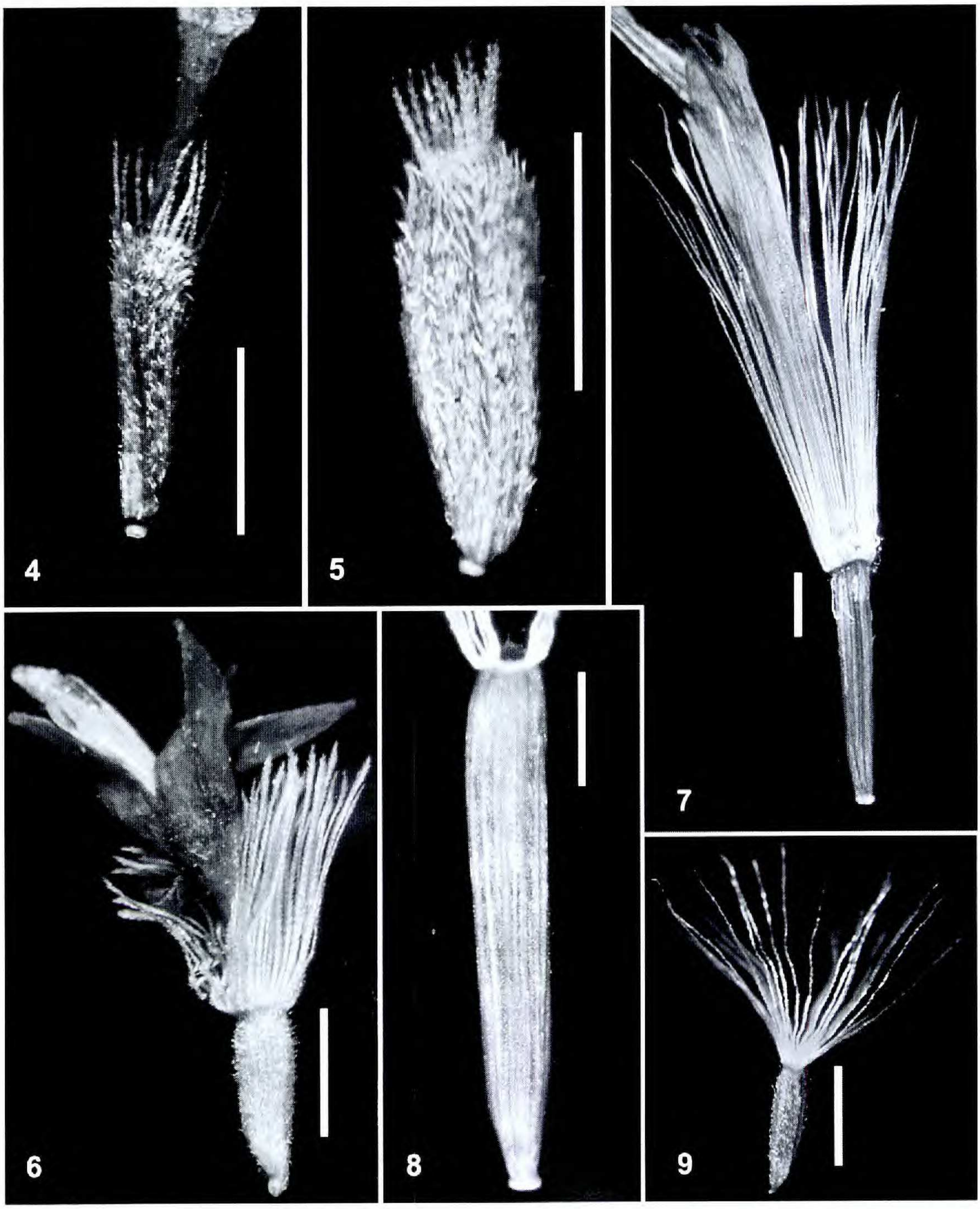
The pappus of the genus *Solidago* is usually biseriate, although obscurely so in some species. In most species the pappus exhibited either alternation of

shorter and longer bristles, alternation of clavate and non-clavate bristles, or some degree of basal overlapping of outer and inner bristles of the primary inner and outer whorls. Table 1 lists observations on the degree of clavateness of bristle tips, presence or absence of evidence of alternation of whorls of bristles, degree of basal overlapping of outer and inner long whorls, and specific observations on 75 species of *Solidago* and 17 species of 14 related genera. Species of *Solidago* are grouped within Table 1 by section, subsection and series following the treatment of the genus by Semple (Semple et al. 1999; Semple 2003; Semple, submitted; Cook and Semple, submitted, treatment of *Solidago* for Flora North America). There is a large range in size of the cypselae bodies and length of the pappus bristles among species of *Solidago* (Figs. 4–9). Bristles can be much shorter than to four times longer than the fruit body, and bristle length ranged from 0.25–7.5 mm. Cypsela bodies varied from 0.5–5 mm in length and from glabrous to densely short strigose. The number of bristles per cypsela ranged from about 25 (Fig. 9 , *S. canadensis*) to more than 40 (Fig. 6, *S. auriculata*). On average, pappus bristles were slightly shorter than the disc corollas (averaging about 9/10 as long comparing the mature pappus to the disc corolla length at anthesis based on data in Semple and Cook, submitted).

Some of the pappus bristles in the majority of species of *Solidago* were observed to be more or less clavate, and these were the primary inner whorl bristles in taxa where position of the whorls could be determined. About 25% of the species examined had, relative to other species, broad clavate bristle tips on the primary inner whorl of bristles, e.g., *S. auriculata* (Fig. 6), *S. erecta* and *S. arguta*. Almost all species exhibited some indication of alternating clavate bristles and non-clavate bristles (Fig. 6), and some exhibited alternating between short bristles and long bristles, e.g. *S. ulmifolia*, (Fig. 13). Alternation of short and long bristles indicated a biseriate pappus even if little difference was observed in tip traits of the two whorls. Variation in the pappus of each species was observed but was of limited range; that is, bristles of a whorl could vary from scores of 0–2 or 3–4 for degree of clavateness, but not to the degree that some fruits had only non-clavate bristles while others of the same species had only strongly clavate bristles.

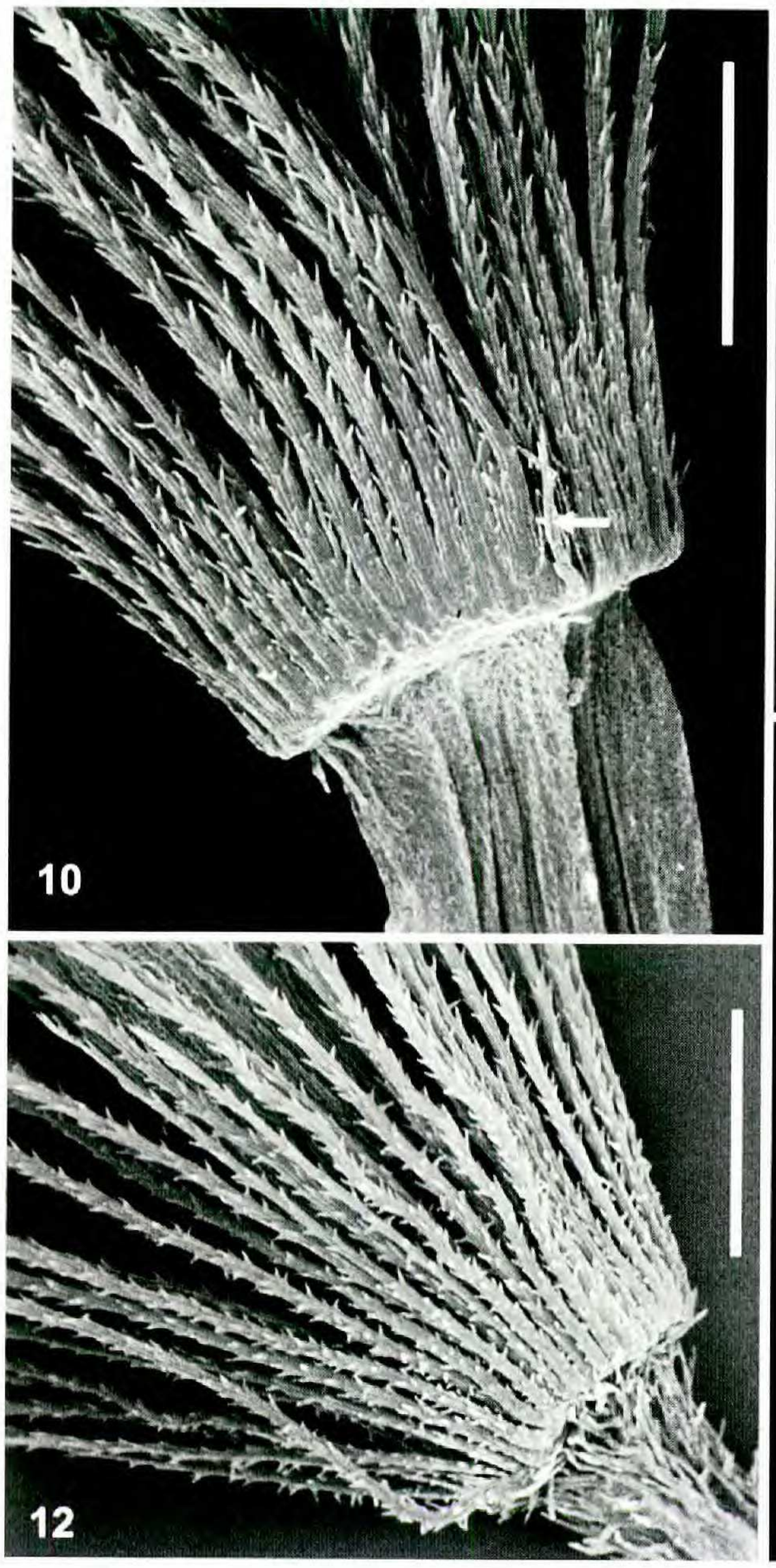
Some species had very clear overlapping of the bases of the primary whorls of bristles, e.g. *S. rigida* (Fig. 10) and *S. odora* (Fig. 12), while others (e.g., *S. bicolor* and *S. ulmifolia*) clearly had overlapping of some bases of the pappus bristles while other bristles on the same fruit did not appear to be overlapping. Many other species exhibited only slight overlapping of the bristle bases (e.g., *S. glomerata* and *S. multiradiata*) or random overlapping of some bristle bases but not in a clear primary inner whorl and primary outer whorl pattern. (e.g., *S. leavenworthii* and *S. simplex*). Some species appeared to have no overlapping bases, e.g. *S. altissima* (Fig. 11).

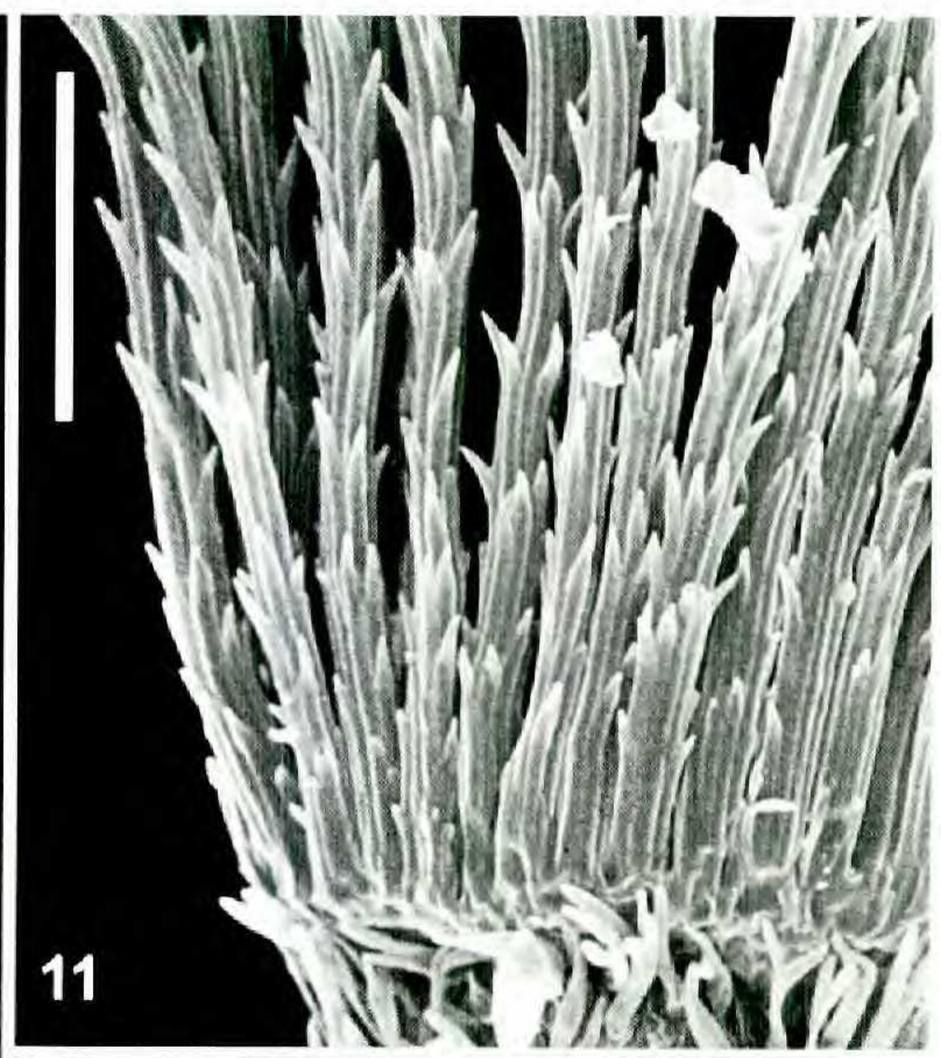
Some species of *Solidago* had a third, much reduced, secondary outer whorl

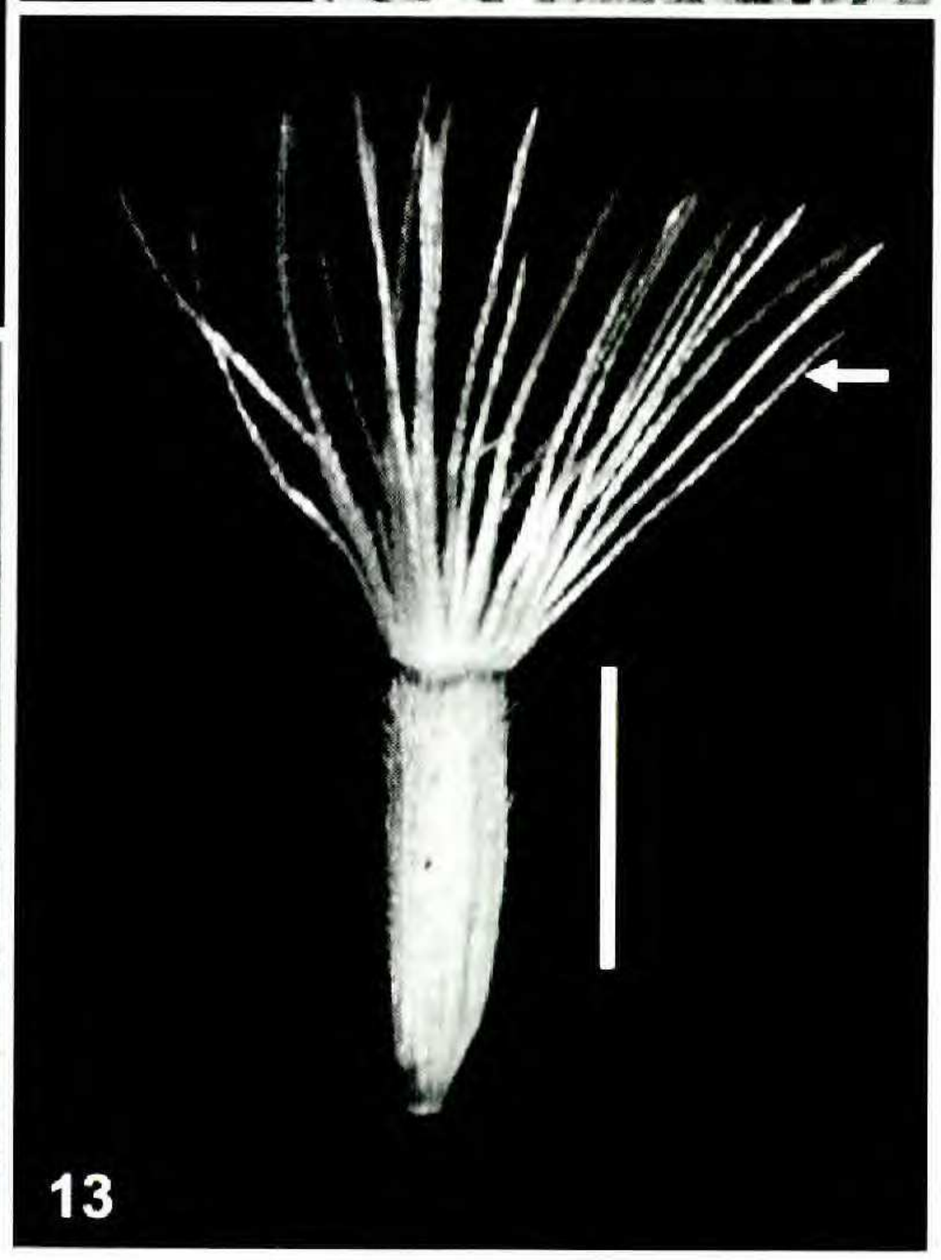


FIGS. 4–9. Length and number variation pappus bristles in *Solidago*; white scale bar = 1 mm. **4–5.** *Solidago sphacelata*, immature and mature cysellae, respectively. **6.** *Solidago auriculata*, maturing cypsela with disc corolla attached, scale bar = 1 mm. **7–8.** *Solidago macrophylla*, immature and mature cypselae, respectively. **9.** *Solidago canadensis*, mature cypsela.

of a few short barbellate bristles: e.g., *S. erecta* and *S. kralii*, *S. rigida* (Fig. 10) and *S. sempervirens*. This condition was difficult to observe and required searching at 70–100×. As noted in the Materials and Methods, detection of the presence of a third whorl was difficult because the few small bristles making up







FIGS. 10–13. Variation in pappus bristle whorls in *Solidago* (scanning electron micrographs). **10.** Biseriate-triseriate pappus, *S. rigida*, scale bar = 0.43 mm; arrow indicates short outer pappus bristle. **11.** Uniseriate pappus, *S. altissima*, scale bar = 100 :m. **12.** Biseriate pappus with clearly overlapping inner and outer whorls of bristles, *S. odora*, scale bar = 0.43 mm. **13.** Biseriate pappus with shorter outer whorl (arrow) and longer inner whorl of bristles, *S. ulmifolia*, scale bar = 1 mm.

the whorl could easily be missed. Thus, other species of *Solidago* than those noted in Table 1 may also occasionally produce a secondary outer whorl. Within the North American Clade of the Astereae a short outer whorl of bristles is known in other species, but it is not always clear whether the short bristles are the primary or the secondary outer whorl, e.g., all species of *Doellingeria*, some species of *Eucephalus*, almost all species of *Erigeron*, most species of the goldenaster subtribe Chrysopsidinae (Semple 1996; Nesom 2000; Semple et al.

2002). In *Doellingeria*, the short outer bristles clearly make up the secondary outer whorl. In other genera, the outer short bristles may be the secondary outer whorl or the primary outer whorl. Additional research is needed on these genera.

Within each section and subsection variation was seen in each of the features examined, but patterns were still present. The strongest evidence for a biseriate nature of the pappus of *Solidago* was observed in members of *S.* sect. *Corymbosae* and in *S.* subsect. *Albigulae*. Members of subsect. *Junceae*, subsect. *Maritimae*, subsect. *Venosae*, subsect. *Triplinervae* nearly always were observed to have non-clavate to weakly clavate bristle tips. In three species in the latter subsection, no evidence of a biseriate pappus was detected: *S. altissima*, *S. canadensis*, and *S. gigantea*. These species had no observable alternation, no clavate qualities to the bristles and no overlapping at the bases.

SYSTEMATICS IMPLICATIONS

The determination that *Solidago* species generally have a biseriate pappus with a primary inner whorl of clavate bristles means the genus is not aberrant within the Solidagininae sensu Nesom (2000). Of the taxa examined, the most distinct pappus was that of *Gutierrezia sarothrae* which had erose scales rather than barbellate and sometimes clavate bristles. The results mean that pappus traits are not useful in separating *Oligoneuron* (= *S.* sect. *Corymbosae* here) from *Solidago*. If authors wish to do so, then the argument will need to rely on other differences. Within the genus *Solidago*, there is sufficient variation in pappus traits among members of subsections and series that pappus traits can not be used as diagnostic features of any infrageneric group with one exception. The very short pappus of *S. sphacelata* is unique and is diagnostic for ser. *Brachychaeta*, if the series is treated as monotypic, as done here. Nesom (1993) defined the series by its cordate to truncate basal leaves with winged petioles, strongly reduced cauline leaves, 0–3 ray florets, and markedly short pappus bristles; he included *S. sphacelata*, *S. auriculata* and *S. brachyphylla*. The bristles of the latter two species are about 2/3 the length of the corollas, while those of *S. sphacelata* are about 1/4 to 1/5 the length of the corollas.

The most obvious conclusion to be drawn is that older descriptions of pappus traits of members of the Astereae may not be accurate or sufficiently detailed. Future descriptions should be based on very careful observations at high dissecting scope magnifications or lower powered compound microscope magnifications. Use of the labels "primary inner and outer whorls" and "secondary whorl(s)" should facilitate and standardize additional research on pappus whorl variation in the Astereae.

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REFERENCES

CORRELL, D. S., M.C. JOHNSTON. 1970. Manual of the vascular plants of Texas. 1970. Texas Research Foundation, Renner.

CRONQUIST, A. 1980. Vascular flora of the southeastern United States – Vol. 1 Asteraceae. The University of North Carolina Press, Chapel Hill.

CRONQUIST, A. 1994. Intermountain flora vascular plants of the Intermountain West, U.S.A: Volume 5 Asterales. The New York Botanical Garden, Bronx.

FERNALD, M.L., 1950. Gray's manual of botany 8th Ed. D. Van Nostrand Company, New York.

GLEASON, H.A. and A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada, second edition. The New York Botanical Garden, Bronx.

HARRINGTON, H.D. 1964. Manual of the plants of Colorado. 2nd ed. Swallow Press, Chicago.

HOLMGREN, P.K., N.H. HOLMGREN and L.C. BARNETT. 1990. Index herbariorum. Part I. The herbaria of the world, ed. 8. Regnum Veg. 120:1–693.

KEARNEY, T.H. and R.H. PEEBLES. Arizona flora. University of California Press, Berkeley.

NESOM, G.L. 1991. Morphological definition of the *Gutierrezia* Group (Asteraceae: Astereae). Phytologia 71:252–262.

NESOM, G.L. 1993. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on the phylogenetic position. Phytologia 75:1–44.

NESOM, G. 2000. Generic conspectus of the tribe Astereae (Asteraceae) in North America, Central America, the Antilles and Hawaii. University of North Carolina, Chapel Hill.

RADFORD, A.E., H.E. AHLES, C.R. BELL. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill.

SEMPLE, J.C. 1996. A revision of *Heterotheca* sect. *Phyllotheca* (Nutt.) Harms (Compositae: Astereae): the prairie and montane goldenasters of North America. Univ. Waterloo Biol. Ser. 37:1–164.

SEMPLE, J.C. 2003. New names and combinations in *Solidago* (Asteraceae: Astereae). Sida 20:1605–1616.

SEMPLE, J.C. (submitted). *Brintonia* E.L. Greene. In: Flora North America Editorial Committee, eds. Flora of North America. Vol. 20. Asteraceae. Oxford University Press.

SEMPLE, J.C. and R.E. COOK. (submitted). *Solidago*. In: Flora North America Editorial Committee, eds. Flora of North America. Vol. 20. Asteraceae. Oxford University Press.

SEMPLE, J. C., G.S. RINGIUS and J.J. ZHANG. 1999. The goldenrods of Ontario: *Solidago* L. and *Euthamia* Nutt. 3rd Edition. Univ. Waterloo Biol. Ser. 36:1–90.

SEMPLE, J.C., S.B. HEARD and L. BROUILLET. 2002. Cultivated and native asters of Ontario (Compositae: Astereae): *Aster* L. (including *Asteromoea* Blume, *Diplactis* Raf. and *Kalimeris* (Cass.) Cass.), *Callistephus* Cass., *Galatella* Cass., *Doellingeria* Nees, *Oclemena* E.L. Greene, *Eurybia* (Cass.) S.F. Gray, *Canadanthus* Nesom, and *Symphyotrichum* Nees (including *Virgulus* Raf.). Univ. Waterloo Biol. Ser. 41:1–134.